

and its more widely spreading perianth segments. Its nearest relationship is probably not with that variety and, if this is true, it has no close relatives. The only other species of this alliance with crested ovaries in eastern North America is *A. Cuthbertii*, which is at once so conspicuously distinct from *A. speculae* that they could not be confused. *A. Cuthbertii* has only two leaves per scape, the processes of the conspicuous crest are contorted, the perianth segments reflexed, and the bracts mostly 5-nerved. Yet, *A. Cuthbertii* seems to be the closest relative of *A. speculae*. Among the western species of this alliance, only *A. Geyeri* seems to be a possible relative. This species, however, has urceolate-campanulate flowers, and the processes of the crest are little more than inconspicuous knobs. The relationship with *A. Geyeri* cannot be close. It seems, therefore, that *A. speculae* represents an eleventh distinct evolutionary line in the *A. canadense* alliance, or that it stands ancestral to *A. Cuthbertii*. The latter hypothesis is particularly appealing. Morphologically, *A. speculae* is intermediate between *A. Cuthbertii* and the less specialized western species, such as *A. Geyeri*. Furthermore, its present distribution fits this hypothesis, inasmuch as it is apparent that the *A. canadense* alliance as a whole radiated from the Southwest. One cannot overlook, however, some resemblance between *A. Cuthbertii* and *A. Plummerae* and the possibility that the latter, although tetraploid, might be the most primitive surviving member of the alliance. This might imply an early separation of the lines which gave rise to *A. speculae* and *A. Cuthbertii*, respectively, so that the former could not stand as ancestral to the latter.

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AN ALTERNATIVE EXPLANATION OF SUBSPECIATION IN ASCLEPIAS TUBEROSA

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Asclepias tuberosa L. (Woodson, 1954) is represented in the southeastern United States by a relatively extensive Appalachian subspecies and a somewhat more restricted Coastal Plain repre-

sentative, a relationship which has been observed repeatedly in many species and genera for some time. It is easily conceived how many such Coastal Plain forms could have originated from Appalachian species some time after the close of the Cretaceous and differentiated in response to ecogeographical factors present in the newly emerging Coastal Plain. However, in such instances, unless isolating mechanisms other than those of ecogeographical character have since become established or unless the ecological barrier is sharply delimited, intergradation is expected between such forms. Yet, Woodson's (1947b) detailed statistical analyses of leaf variation in *Asclepias tuberosa* revealed that this intergrading zone presently evident between the Coastal Plain subsp. *Rolfsii* and the Appalachian subsp. *tuberosa* is due to hybridization between the two subspecies and not to an ecogeographical differentiation into a cline. This led Woodson (1947a) to conclude that *Rolfsii* must have originated independently in more or less complete isolation from *tuberosa*. To account for this, Woodson then postulated that *Rolfsii* evolved on Orange Island, a hypothetical island or archipelago in north Florida during Oligocene times. Since Woodson's account of the supposed origin of *Rolfsii* has been considered biological evidence substantiating the existence of a functioning Orange Island Refugium by Woodson, Thorne (1949), and others, it seems highly desirable to explore other ways in which this subspecies could have originated lest we find ourselves relying too freely and perhaps unjustifiably at times on this Island as a refugium.

Granted the occurrence of hybridization between the subspecies of *Asclepias tuberosa*, how then can one account for this apparently independent origin of *Rolfsii* by means of the known processes of ecogeographical subspeciation? As Woodson pointed out, "*Rolfsii*, surely, could not have maintained a separate existence with *tuberosa* upon the Appalachian upland, later migrating to Florida only to return in panmixy with its sister subspecies."

The Coastal Plain today is a geographical province differing considerably from the adjacent and generally more mesic Pied-

mont and Appalachian provinces. Since the habitats of the Coastal Plain presumably developed gradually through a successional series over a period of time, it seems reasonable to assume that these differences (notably the edaphic ones) could only have been more striking when the Coastal Plain was in its initial phase of exposure. This would mean that the genetic system of the pioneering Coastal Plain element of *tuberosa* would have been selected under much more rigorous and quite different conditions from those prevailing today. It possibly required considerable time for a genetic system to evolve from the parental species which was sufficiently adapted to be aggressive in this newly available environmental complex. But once such biotypes had evolved, they could migrate southward as rapidly as the successional stages and dispersal would permit since environments characteristic of the succeeding portions of the Coastal Plain would be very similar to the first to which the invading element must necessarily have been adapted. The rapidity with which this genetic element migrated away from the parental stock would result in a progressively more effective geographical isolation, thus accounting for the apparently independent evolution of *Rolfsii* in more or less complete isolation. (Although not the case in *Rolfsii*, this could provide conditions facilitating the evolution of other isolating mechanisms). The basis of the reasoning employed here is dependent upon the following tenets:

The less favorable a newly available area is for occupancy and invasion by organisms of an adjacent area,

1. the less the probability of the presence of existing biotypes which can immediately invade the new area,
2. the greater the difference there will be in the genosystem of a derived race which can invade the new area,
3. the greater the probability of a longer period of time required for the evolution of this genosystem,
4. the greater the differential in rate of migration between the best adapted and the least adapted biotypes of this genosystem,
5. the greater the degree of morphological and physiological differentiation and/or specialization of the invading race,
6. the greater the effectiveness of ecogeographical isolation (if such isolating mechanisms are involved.)

7. the longer the newly evolved race can maintain a separate identity from the parental species.

The genetic system of *Rolfsii* is presumably a specialized one derived from only a part of the broader genetic system of *tuberosa*, and one which, perhaps, has become even further specialized. There would then be little or no pressure on a northward movement of *Rolfsii* genes into *tuberosa*. There would be, however, continued forces operating at the juncture of subspecific differentiation on a flow of *tuberosa* genes southward just as there had been since the time of exposure of the Coastal Plain. Furthermore, as the Coastal Plain became more mature it offered more variety and less severity in habitat; consequently, many *tuberosa* genes and gene complexes which previously were insufficiently adapted to that environment could then flow southward in addition to some of the previous ones. This would result in an invasion of the Coastal Plain *Rolfsii* by increasingly less differentiated biotypes of *tuberosa* which could then hybridize with the remaining *Rolfsii* element in that area of the Coastal Plain where subspeciation was first initiated. This progression of secondary invasion elements of *tuberosa* would then tend to absorb *Rolfsii* and could then account for the present hybridization occurring between the two subspecies.

If *Rolfsii* were ever present in the Carolinas and northward it has apparently since been absorbed by *tuberosa*. It is of interest to note in this connection that geological evidence suggests that a considerable portion of the Carolina Coastal Plain has been exposed and available to plants since the end of the Cretaceous. At the present time, *Rolfsii* appears to be losing its identity throughout the remainder of the Coastal Plain with the exception of peninsular Florida which is farthest from the presumed point of origin.

This analysis, of course, does not disprove the possible existence of an Orange Island Refugium. It is merely an attempt to offer an alternative explanation of subspeciation in *Asclepias tuberosa* which could account for the hybridization presently occurring between the subspecies without having to rely on an Orange Island Refugium.

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NOTES ON THE DISTRIBUTION OF OHIO COMPOSITAE: II. EUPATORIEAE, SENECTIONEAE, CYNAREAE, CICHORIEAE

ROBERT W. LONG

This is the second paper of a series of three that presents some results of a recent study of Ohio Compositae. In part I¹ it was noted that plants discussed in these reports are ones whose occurrence in Ohio is questionable, judging from information given in Gray's Manual (1950) and The New Britton and Brown Illustrated Flora (1952). For the present, the nomenclature is derived chiefly from Gray's Manual, but this does not imply it is necessarily the best treatment for the taxa listed.

All specimens and county records cited here are deposited in the Herbarium of The Ohio State University, and the identifications have been verified by the writer.

EUPATORIEAE

Eupatorium album L. var. **glandulosum** (Michx.) DC. This variety is easily separated from the typical one by the occurrence of minute, dark glands on the phyllaries; thus, the variety is quite distinct. Its presence in southern Ohio represents a northward extension of the range given by Fernald. COLLECTION DATA: Jackson Co., Liberty Twp.,

ROBERT W. LONG. Notes on the distribution of Ohio Compositae: I. Heliantheae, Anthemidae. RHODORA 60:125-128. 1958.